OCCURRENCE OF THE FRESH-WATER MEDUSA, LIMNOCODIUM, IN THE UNITED STATES.[1]

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In a preliminary note to *Science*, which appeared in the issue of November 8 (1907), attention was directed to the occurrence of *Limnocodium* in this country, and some brief account given of this circumstances and conditions of its appearance. As indicated in that report a few living specimens came into the possession of the writer through the courtesy of the United States Bureau of Fisheries, and were kept alive and under observation for a period of some ten days. Since it was confidently anticipated that a further supply of specimens would be received very soon no particular care was taken to prolong the life of the first supply. A few were used for some simple experiments, to be described in a later section, and some preserved for histological purposes. It is with extreme regret that I have to record the utter failure of attempts to secure a further supply of living specimens, though from no particular blame of those concerned. At least one lot was forwarded to the writer at Syracuse, and left Washington in good shape, but from some cause not clear all were dead when received, having perished in transit. Other supplies were immediately sought, but within a few days the very disappointing advice was received from the director of the aquarium that the medusæ had suddenly disappeared. Quoting his own words: "When I went to the tank where they have been so plentiful for the past eight weeks there was not one to be seen, and apparently they have disappeared as mysteriously as they came. Possibly on account of the cold weather they may have gone to the bottom of the tank, among the pipes where I cannot get them, but if I discover them again I will advise you at once." This letter bore date of September 27. In a later letter, December 3, I was advised that no specimens had appeared during the interval of two months, and from the history of these medusæ in Europe this is only what might have been anticipated. Therefore, with the first chapter

[1] Contributions from the Zoölogical Laboratory, Syracuse University.

of the present case thus closed, the details, so far as known, may properly be formulated and made available.

Locality.

The medusæ were discovered in the aquarium of Mr. W. B. Shaw, a florist, who for many years has cultivated various aquatic plants, among them several species of tropical, or subtropical water lilies, *Nymphæa zanzibarensis*, *Cabomba* (*Caroliniana ?*), and a species of *Ludwigia*. But, *all these were reared from seeds*, no grown plants having been at any time imported or introduced into the tanks. And at no time has the *Victoria regia* been grown here, a fact of no small interest in relation to earlier suggestions as to the problem of the transportation of the medusæ from tropical waters.

The hot-house contained in all six tanks, each three feet wide, three feet deep, and about twelve feet long. These were all stocked in the same way, and with about the same sorts of plants, and a species of Paradise fish. The aquaria are of the balanced sort, and have been in use for some six or eight years without material change of water or organisms. The aquaria are used chiefly during the winter by Mr. Shaw including late fall and spring, for the purpose of carrying over certain of the more delicate tropical plants from season to season, and stand idle during summer, water being added to replace the loss due to evaporation.

Of these six tanks, alike in construction, water supply, and other features, medusæ appeared in *one only*, and that about midsummer, flourishing during the hot weather and promptly disappearing with the approach of autumn cold. When first discovered they were in considerable numbers and of various sizes "some as small as a pin's head and some one fourth inch in diameter." The largest specimen which came to my hands measured about 9 mm. in diameter by 4 mm. in height of bell.

Hoping to obtain some clue as to the hydroid stage I obtained through the courtesy of the Bureau of Fisheries a collection of various plants growing in the tank, with scrapings of algal slime and other debris from the sides and bottom of the tank. This was promptly and carefully examined on arrival, and frequently

during succeeding days, but no trace of a hydroid was found. The material was kept in my laboratory, which has a fairly constant temperature, for several weeks, indeed months, and repeated examinations made from time to time, but no trace of any hydroid form appeared, though species of Protozoa and rotifers continued to live and thrive quite normally. Such are the facts as to locality and conditions under which the medusæ were found. Their similarity to those concerned in the appearance of the same medusa in London many years ago is quite striking. Its occurrence later at several places on the continent has been recorded by several observers. The most recent is that of its appearance at the botanical garden at Munich in the basin containing the giant water lily, *Victoria regia.* Boecker's account, which appeared in the *Biologisches Centralblatt* (Bd. XXV., p. 605, 1905), agrees in most respects with the earlier records, and with the foregoing as well. He regards the Munich species as probably identical with *Limnocodium sowerbii*, the occurrence of which in the Victoria tanks of Regents Park, London, had been variously described by Lankester (*Quar. Jour. Mic. Sci.*, Vol. XX., 1880), Allman (*Jour. Linn. Soc.*, Vol. XV., 1881), and Gunther (*Quar. Jour. Mic. Sci.*, Vol. XXXV.). Some further notice will be taken of Boecker's records in a later connection.

General Features and Relations.

The Washington species agree in most respects quite closely with the original descriptions and figures of *Limnocodium sowerbii*, of Allman and Lankester. As compared with the verbal description of Boecker (*op. cit.*), there are some slight differences. For example, he says that the Munich species are characterized by a rather high-arched bell. In my species the bell is rather low, often disc-like. Figs. 1, 2, 3, 4, drawn from life in different aspects, will make this point more evident and striking. However, this difference I do not consider of very great importance.

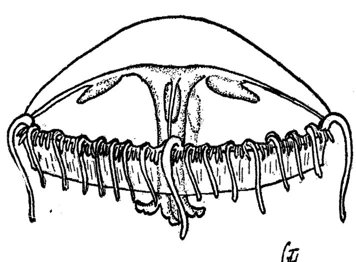

Fig. 1.

Several things might conspire to emphasize or exaggerate it. As is well known, age has much to do with the shape of hydrome-

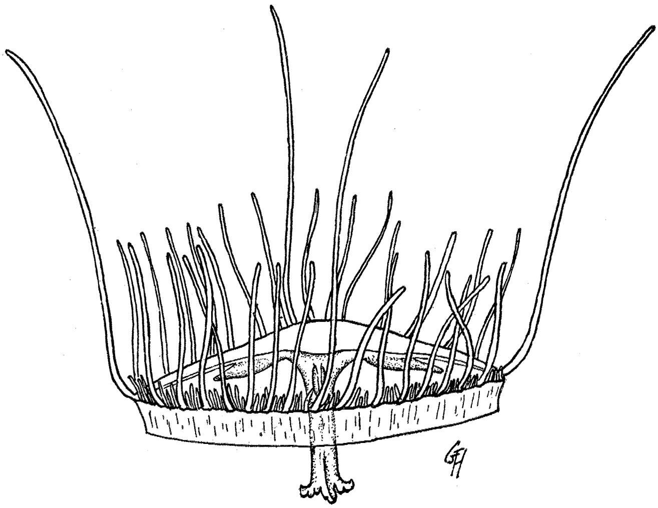

FIG. 2. Medusa, floating aspect.

dusæ, young specimens often being hemispherical, while at maturity they may become quite disc-like. Again, there are often marked individual differences which have to be considered in estimating the mean shape of the species. Further, preserved specimens are almost always more or less contracted, and hence may seem to be much more highly arched than is the case in life.

It should be observed in this connection that the specimens shown in the figures present very different aspects. Fig. 1 represents the medusa in an average swimming attitude, the tentacles more or less contracted, the manubrium somewhat contracted, and the bell rather higher than shown in Fig. 2, which represents the creature in the floating attitude, body and organs generally

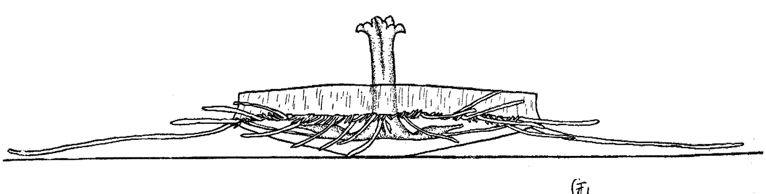

FIG. 3. Medusa, resting normally on bottom of aquarium.

extended, and more or less passive. In Fig. 3 the specimen is represented in a rather characteristic state of repose often observed, resting on the exumbrellar surface on the bottom of the aquarium. Here again, the creature is in a condition of general relaxation, the manubrium extended and in position to take such prey as may come within its reach. The tentacles also are much extended, a condition quite common when in this pose.

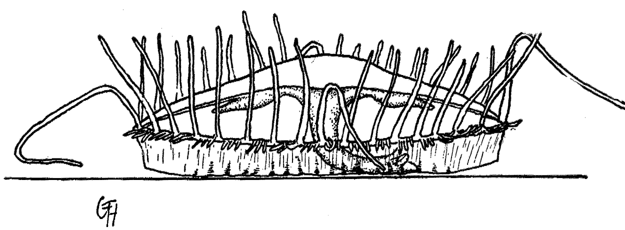

FIG. 4.

In Fig. 4 is shown a less familiar attitude of the creature. Though not especially rare, the position seems to indicate a condition of fatigue, though the tentacles are more or less erect. A comparison of the several figures, representing as closely as possible the living aspects of the creature, will show the general relation of tentacles, velum, manubrium, shape of bell, etc., to the state of activity or repose, as the case might be.

TENTACLES.

There are four perradial tentacles, conspicuous as to size and length, as shown in the several figures. In certain cases it was possible to distinguish apparently, a series of four interradial tentacles though they were not conspicuously differentiated as to size or length. The tentacles are quite numerous, especially in older specimens, and arranged in several series, younger ones arising from the lower, or proximal portion of the margin. While the aspect exhibited by these organs in the figures might seem to indicate more or less rigidity of structure, this did not appear to be the case in the living specimens. They were quite flexible and highly contractile.

In describing the tentacles of the Munich specimens Boecker (*op. cit.*) was unable to confirm the account given by Günther as

to the insertion of the base into the gelatinous margin of the bell, believing them to be quite free. He does not state whether he had studied this feature in sections, or from simply observing the living specimens.

On this point my specimens show considerable differences. In the living condition, the larger tentacles, while capable of great freedom of movement, are yet inserted in notch-like depressions in the margin, as shown in Fig. 5. As studied in sections they

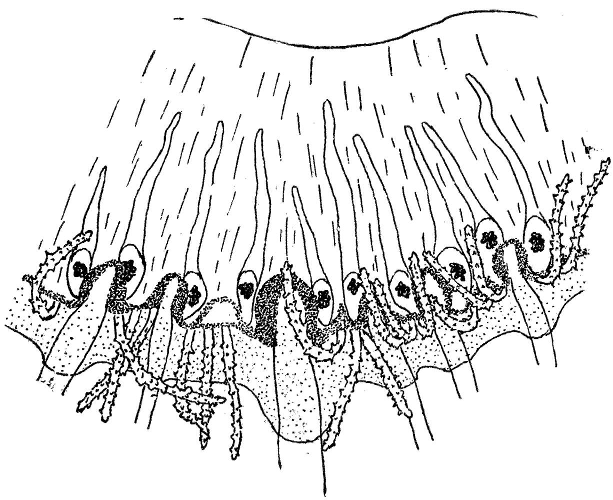

FIG. 5. Portion of margin enlarged, showing tentacles, velar canals and marginal bodies.

show something of the condition figured by Günther, though very much less marked, the degree of adnation being much less than in his description. Furthermore, I should not consider the degree of fusion as having any very evident relation to the aspects of the tentacles exhibited by the living medusæ. On the contrary, the varying aspects of these organs under differing conditions of activity or repose are such as to strongly suggest a very different conclusion and interpretation.

A further tentacular feature remains to be considered, namely, that of structure. Both Allman and Lankester described the tentacles as solid, though differing more or less from that found in other medusæ with solid tentacles. Günther has later shown that these conclusions were erroneous, and attributes

the error as possibly due to an examination of very young tentacles, or to tentacles in a state of high contraction.

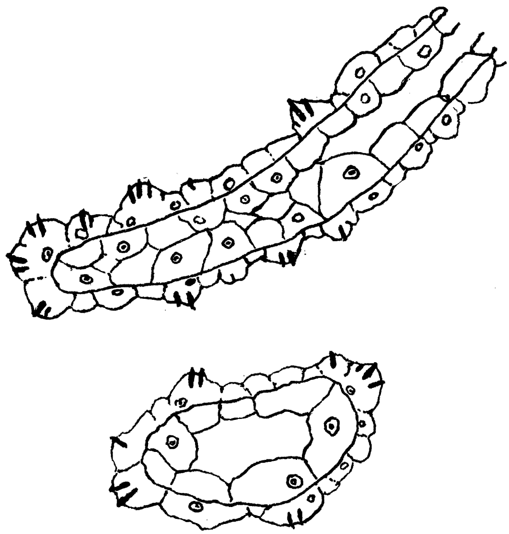

FIG. 6.

My own sections confirm the results of Günther. In sections of very small tentacles it is quite difficult to distinguish the lumen of the tentacular axis. But in larger specimens this is quite easily demonstrated, and it seems rather strange that two such capable observers should have failed to recognize this feature. Fig. 6 shows camera sketches of both cross, and long sections of tentacles, and Fig. 7 is a photograph of the terminal portion of a tentacle made under the microscope.

FIG. 7. Tentacle of Limnocodium.

In this connection I desire also to point out that in none of my specimens have I found the very marked papillated aspect of the tentacles as represented by both Lankester and Günther (*op. cit.*), and later by Browne (*Quar. Jour. Mic. Sci.*, Vol. 50, Fig. 3, pl. 37). These papillæ are specialized organs bearing nemato-

cysts, according to these observers. But I have failed to find any well defined cases of such highly specialized nematophoric structures. The figures, both from the drawings and the photograph alike, confirm this statement. I cannot resist the impression that the figures of the former must have been drawn from greatly distorted specimens due in part perhaps to mode of preservation, or that they may have been made from very young tentacles in which the nematocysts are relatively more conspicuous. A comparison of various of my specimens fails to reveal any essential differences, even where various modes of preservation were employed. An examination of the specimen represented in Fig. 7 will show fairly well the general distribution of the nematocysts, and also the tendency to an annular disposition similar to that common to other hydromedusæ.

Marginal Bodies and Velar Canals.

Concerning these organs I have made no attempt to critically investigate anew their structure or development, beyond a more or less careful review of the work of Lankester, and the later work of Günther (*op. cit.*). So far as I have gone my observations confirm that of the previous investigators. Fig. 5 is a camera sketch of a portion of the margin and velum showing the general aspects of the several organs, tentacles, marginal bodies and capsules, and velar canals. But while confirming the facts described by Lankester as to the structure and relations of the marginal bodies, I have found no convincing evidence of his rather dogmatic assertion that "The refringent body is nothing more nor less than a modified tentacle." This may have sufficed its author at the time it was made, and was quite in harmony with then current views concerning these organs in general. But the time has long since passed when the mere matter of similarity of structures, real or imaginary, is any sufficient warrant for the vaulting conclusion involved in the above quotation. In another connection (*Jour. Exp. Zoöl.*, Vol. I., p. 86), I have taken occasion to question the long current assumption that in Scyphozoa the rhopalia are metamorphosed tentacles. Later observations have only served to deepen the conviction, and I believe adequate investigation will confirm the view that these organs are not, in

any strict morphogenic sense, directly derived from tentacles, particularly such bodies as those here under consideration.

Reproduction.

There is nothing to add to the former announcement as to this feature. Only male specimens have been found. These were in various stages of maturity, some quite young, others sexually mature, with gonads bursting with ripe spermatozoa. In the absence of additional facts there is no particular call for speculations as to the significance of this singular sexual phenomenon.

Affinities of the Medusæ.

Concerning the question of the specific or generic relations I find little occasion for difference of opinion or doubt. That our specimens belong to the genus *Limnocodium* seems thoroughly clear and certain. That it is also specifically identical with the European species, *L. sowerbii* Lankester, seems almost equally certain. I have pointed out certain features of difference, such as the shape of the bell as compared with Boecker's description, and peculiarities of tentacular structure, rather sharply different from those described by the earlier observers. Yet neither of these, nor both combined are such as to warrant the probability of a distinct species. Hence the suggestion made in my preliminary report may be here reiterated, namely, that the American species is almost certainly *Limnocodium sowerbii*.

The following characters may be regarded as fairly diagnostic of the species: Bell rather low, two or three times as broad as high, discoid in shape, especially when floating freely as shown in Fig. 2. Size from 5 to 9 mm. in diameter, by about 4 mm. in height, or less in average specimens; radial canals four, rather capacious, extending from stomach to marginal canal, which is triangular in shape and large; gonads four, suspended from the radial canals about midway between the stomach and margin, pouch-like in shape with the smaller or distal end free, as shown in the figures, pale greenish in color; manubrium long, and with four more or less crenulated lip-like lobes which are of greenish tint, and extending usually considerably beyond the velum; tentacles very numerous, the four perradial ones being conspicuously

long and usually extended upward over the bell in graceful curves; other tentacles in several cycles, the newer arising along the inner edge of the margin; the older ones set in notch-like scallops about the margin, as shown in Fig. 5. The general color of the bell translucent, or of faintly bluish tint by reflected light. Bases of tentacles surrounded by a dull brownish, but inconspicuous pigment.

Experimental.

The extensive experimental work which has been done upon medusæ within recent years, and the various results which have been obtained by different experimenters, at once suggested the desirability of repeating certain phases of it upon a fresh-water medusa. Accordingly I devised a series of experiments to test its regenerative capacity along lines similar to those made by the writer on *Gonionemus*, *Rhizostoma* and others; to test its behavior in response to various stimuli — photic, chemical, mechanical, tactile, etc. Having received less than a dozen living specimens in the first lot it was of course out of the question to set about any systematic and extended experimentation at that time, fully anticipating ample material later for the work planned. As already intimated in the introduction, these plans were doomed to miscarry, owing to the utter failure in securing the necessary material for their realization, and but for a single series of very simple experiments this feature of the work would have been wholly lacking. The experiments alluded to had to do wholly with the reaction of the medusæ to distilled water.

The numerous experiments to determine the rôle of certain salts in relation to the rhythmic movements of medusæ are too well known to call for extended review. On the one hand it is claimed that the presence of certain ions (Na), is the all-important factor in arousing and sustaining the movements, while the presence of certain other ions (Ca, K), have an inhibitory effect upon them. "Na ions start or increase the rate of spontaneous rhythmical contractions; Ca ions diminish the rate or inhibit such contractions altogether."

On the other hand it has been claimed that Mg ions are the magic factor which causes the organism to perform its rhythmic

play. Still others have contended that various species react very differently to a given stimulus, and that an element which may prove a stimulus in one case may prove inhibitory or even toxic in another case. It is quite certain, therefore, that the last word has not yet been said concerning this perplexing problem. And so far from the rather dogmatic declaration that "it is only the presence of Ca ions in the blood which prevents the muscles of our skeleton from beating rhythmically in our body" we may better assume an attitude of open skepticism, or at least suspend judgment long enough to perform a few more experiments! In the lack of material for such experimentation in the present case it occurred to me to try in a very simple fashion the effects of perfectly pure, that is distilled, water on the medusæ. In the absence of the ions of the aforementioned elements, Na, Ca, K, etc., in such water should we get any of the results usually attributed to them? The problem seemed simple enough, but not too simple to be unworthy of a trial. Accordingly the following experiments were made:

1. Specimens were transferred from the water in which they had been sent from the aquarium to that of the ordinary tap-water of the laboratory in order to see whether any appreciable effect would follow. But none could be observed; hence they were thereafter freely transferred to such water as circumstances seemed to suggest from day to day. Later tests of this water showed it to be so free from any of the salts in question as to be indistinguishable by the ordinary chemical tests.

2. A single specimen was next transferred to a jar of distilled water. It moved rhythmically for thirteen beats, then paused. Then followed six beats succeeded by another pause of longer extent during which it floated downward sinking to the bottom. Here there followed five beats and a pause of five minutes. At this time it was transferred back to normal water with the result of prompt resumption of rhythmic activity, but of a more rapid rate, nearly or quite twice that before the experiment was begun. This continued for nearly ten minutes, when the rhythm gradually returned to the normal rate.

3. Another specimen tested in the same way gave almost identically the same reactions.

4. The next specimen, somewhat larger than either of the former, was transferred to distilled water, and pulsed rhythmically twenty-three times, then paused as had the former. Then followed thirteen pulsations with another pause of similar extent, during which it gradually sank to the bottom where it remained motionless for three minutes. It then resumed its rhythmic swimming and continued without further pause for ten minutes when it was returned to the normal water.

5. After about twenty-five minutes all three specimens were transferred at once to a fresh jar of distilled water. In this case the reactions were similar throughout, though with certain individual differences such as one might expect. All swam rhythmically for a half minute, and then paused as in the previous cases. The rhythm was resumed and after a brief time two of the specimens paused again, and as before sank to the bottom of the jar, the third continued swimming. After a short rest those on the bottom resumed their swimming, and all continued for nearly half an hour, just as in normal water. They were left in that condition for twenty minutes longer, when two were found to have sunk to the bottom once more and seemed to show sign of discomfort, such as the contraction of the tentacles, drawing in of the margin of the bell, etc. The third while still swimming, was evidently showing unusual signs of fatigue, the movements being more or less feeble and uncertain. All were at once transferred to normal water. Two soon showed signs of recovery, the third however, continued in a state of collapse and failed to further recover. All had evidently been injured by the long period in the distilled water, and one fatally, since it was later found dead without indications of any recovery in the normal water.

Such in briefest outline are the facts resulting from the few experiments made. It should be stated that they were variously repeated, and with such degree of constancy in behavior as to suggest their perfectly trustworthy nature. Still other experiments of the same sort would have been made, but for the confident anticipation of a large supply of fresh specimens.

In reviewing the literature of this medusa it has been gratifying to find that some experimental work had long ago been done

upon it. In 1880 Romanes (*Nature*, June 24, also "Jelly fish, Star fish, etc.," 1885), whose experiments on various medusæ are well known classics, took occasion to repeat certain of them on *Limnocodium*, chiefly in relation to light, temperature, tactile localization, and reactions to sea water. In most respects he found the reactions of *Limnocodium* comparable in almost every respect with those performed on marine species. His experiments in transferring the specimens to sea water was to test their tolerance to a medium and environment to which their supposed ancestors must have long been familiar, are interestingly the very opposite of those above described. He had previously proved that marine species were unable to endure a transfer for more than ten minutes to fresh water, seldom for more than five, and then with evident signs of more or less severe injury. In the reverse tests with *Limnocodium* he found that no reaction was apparent for about fifteen seconds, when a more or less sudden collapse resulted, with tetanus-like spasms of increasing intensity till all sensory reaction ceases, and after a short time death ensues. An exposure to sea water for even one minute may end fatally, even if the creature be promptly returned to fresh water. Similar results followed an immersion in dilute sea water though with less promptness. In very reduced sea-water ($\frac{1}{10}$), spontaneous activity may continue for some time, but with gradual decline till but slight response is given to stimuli.

In conclusion he states "It will be seen from this account that the fresh-water medusa is even more intolerant of sea water than are the marine species of fresh water. It would appear that a much less profound physiological change would be required to transmute a sea water jelly fish into a jelly fish adapted to inhabit brine than would be required to enable it to inhabit fresh water. Yet the latter is the direction in which the modification has taken place, and taken place so completely that the sea water is now more poisonous to the modified species than is fresh water to the unmodified. There can be no doubt that the modification was gradual — probably brought about by the ancestors of the fresh-water medusa penetrating higher and higher through the brackish waters of estuaries into the fresh waters of rivers, and it would, I think, be hard to point to a more remarkable case of

profound physiological modification in adaptation to changed conditions of life."

In the summer of 1905, as already pointed out, this medusa appeared in considerable numbers in the aquaria of the Botanical Garden of Munich. In a recent paper (*Zeits. f. allgemeine Physiol.*, Bd. VII.), Maas has recorded a series of experiments made to test the reactions of the medusæ to various stimuli, chiefly chemical and mechanical, with brief references also to the influence of temperature. Experiments made with physiological salt solution confirmed in a general way those of Romanes already considered. For example, specimens when first placed in the solution showed quickened, spasmodic and heterochronous contractions, followed later by collapse and finally by death. If left in the solution for only ten minutes and then returned to the normal water the irregularity gradually disappears and the pulsations become synchronous and normal. That these reactions were not due to any difference in temperature he proves by control experiments made on various specimens at the same temperatures in fresh water, and even in water at very much lower temperatures.

He also tested the reactions of emarginated specimens in the salt solutions and found the same spasmodic contraction as observed in the uninjured specimens. A brief summary of the comparative effects of KCl and NaCl is given, from which it would appear that the former tends to inhibit reactions, while the latter serves as an active stimulus, though of a very irregular or heterochonous character.

Maas also points out the somewhat conflicting results of Loeb's experiments on *Gonionemus* and *Polyorchis*, those of Bethe on *Olindias*, and Herbst on *Obelia*; and concludes that among marine medusæ there must be essential differences in their chemico-physical relations.

In the transfer of a delicate creature, such as medusæ, from a medium like sea water to that of fresh water it might naturally be expected that reactions more or less remarkable should occur. But what shall be said of similar reactions which follow the transfer from a fresh-water medium, where if any soluble salts be present it must be in homœopathic doses of high attenuation,

to distilled water devoid of any trace of these elements? Surely it can hardly be claimed here that continued rhythmic action, or its inhibition, is attributable in any specific way to the ions of *this*, *that*, or *any* sort! Possibly those who would vindicate the ion hypothesis at all hazards might assume, as a desperate measure, that certain infinitesimal quantities of these elements may have been carried over in the tissues of the medusæ in their transfer from the normal to distilled water! But the assumption is so wholly gratuitous as to preclude serious consideration.

The writer has no theoretical views to promote or defend. But face to face with the facts he assumes, what is the right of every investigator, namely, freedom to discard any hypothesis which fails to account for his facts, and in so doing the further duty of exposing its futility. A comparison of the experiments heretofore set forth, and those to which direct reference has been made, together with others of similar nature and involving similar methods, shows such degree of confusion, not to say absolute contradiction, in the results obtained, as to suggest pause and serious reflection before any hasty leap be made in formulating conclusions. There is an old, but reputable, saying though involving something akin to paradox: "If the light that is thee be darkness, how great is that darkness." In the light of existing darkness concerning the problem under consideration might not some modium of scientific modesty and hesitation well replace something of the arrogance and dogmatism which have bulked so large in recent literature of these problems?

SYRACUSE UNIVERSITY,
February 25, 1908.